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9 Pozo et al. • Hunting Effects on Red Deer Antler Size

10 **MODELLING THE IMPACT OF SELECTIVE HARVESTING ON RED DEER**
11 **ANTLER SIZE**

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ABSTRACT Hunting is a common component in the management of ungulate species. Despite its widespread use, the influence of selective harvesting on phenotypic trait change is still ambiguous, and represents a critical gap in our understanding of the responses of wild populations under harvest. Using the long-term red deer (*Cervus elaphus* L.) dataset from the Isle of Rum National Nature Reserve, Scotland, we assessed the relationship between antler length and key demographic processes (survival, recruitment, antler growth and parent-offspring trait correlation) for the male component of the population. We then constructed the first integral projection model (IPM) for this species to examine the effects of simulated trophy hunting on two population-level parameters: the stable antler size distribution and the reproductive value of males. When male mortality rates due to hunting were below 20% the effect on antler size distribution and the reproductive value function were relatively small. However, as mortality due to hunting increased to 50% in large individuals, the direct effects of hunting on mean antler size and reproductive value increased markedly. Our model acts as a useful starting point to investigate the ecological and evolutionary consequences of hunting in red deer.

KEY WORDS antler size, integral projection model, Isle of Rum, sexual selection.

Wild ungulates have been hunted for centuries, however the consequences of their exploitation remain unclear. In particular, the influence of selective harvesting on phenotypic change is not well understood, and represents a critical gap in our knowledge of the responses of wild populations to harvest. Trophy hunting represents one form of selective harvesting that has been traditionally implemented in wild cervids. This harvesting regime is a non-random process whereby humans select individuals to be removed from a population based on one or several phenotypic traits (Festa-Bianchet 2003; Mysterud 2011). Typically, males with the largest trophies (e.g. antlers or horns) are sought and removed from the population, imposing an unnatural mortality rate on prime-age males (i.e. those that have attained

asymptotic body mass prior to senescence) or young adults (Gaillard et al. 1998; Monteith et al. 2013). This harvesting regime can result in negative demographic consequences including changes in population structure (Traill et al. 2014), skewed sex-ratios (Ginsberg & Milner-Gulland 1994; Milner-Gulland et al. 2003) and decreased antler and/or horn size (Monteith et al. 2013; Milner et al. 2007). Such deleterious effects have been observed in both bovidae (Pérez et al. 2011; Festa-Bianchet et al. 2014) and cervidae (Monteith et al. 2013).

Antler size is often under natural and sexual selection. In wild populations of deer, males differ markedly in their fertility rates (Malo et al. 2005a) and antler size (Kruuk et al. 2002), with adult males with larger antlers attaining highest breeding success (Clutton-Brock 1981; Andersson 1994; Kruuk et al. 2002; Malo et al. 2005b). In addition, the key role of antlers in male-male combat (Clutton-Brock 1982; Andersson 1994) suggests that individuals with larger antlers may live longer (Lemaître et al. 2014). Since sexually selected characters are by definition under selection, any unnatural intervention that changes mortality or reproductive schedules of individuals with specific trait values has the potential to generate evolutionary change. Harvest by humans has been shown to cause changes in phenotypic traits (Darimont et al. 2009), and even to generate evolutionary change (Palumbi 2001). Trophy hunting can therefore be expected to impose selective impacts on wild populations. One way to investigate this is to evaluate how hunting is likely to influence fitness. We do this here by examining how hunting might impact not only the distribution of trophy sizes within the population, but also the reproductive value – a quantity describing the expected representation in terms of descendants across all trait values of an individual with a specific character value in the future population (Fisher, 1930).

Artificial removal of males with large trophies will likely lower both the reproductive value of large individuals and mean trophy size within the population. However, trait size response to trophy hunting has not been consistent across species, and in many cases

environmental factors play a much stronger role on mean values than selective removal (Schmidt et al. 2007; Myrsetrud 2011). However, other studies have suggested that phenotypic change in hunted populations can also be due to an evolutionary response (Coltman et al. 2003).

In long-term studies of individual life histories, experimental culling of individuals often conflicts with other research interests and cannot therefore be used to test harvesting hypotheses. As a result of this, the use of matrix models to represent population structure has become popular (Caswell 2001; Coulson 2012; Ellner & Rees 2006). In particular, integral projection models (IPMs) – a generalisation of matrix models – have been developed to study and track the dynamics of continuous characters (Easterling, Ellner & Dixon 2000; Coulson 2012). IPMs can be parameterised directly with observational data (Ellner & Rees 2006), and enable key population-level parameters, such as a stable phenotypic trait distribution and reproductive values, to be predicted from individual-level data (Caswell 2001). Importantly, IPMs can be perturbed to simulate harvesting regimes in wild populations and have provided reliable information on how demographic parameters change within and between age groups (Traill et al. 2014).

In this study, we use individual based data on the red deer (*Cervus elaphus*) from the Isle of Rum National Nature Reserve, Scotland (Clutton-Brock et al. 1982, Pemberton et al. 1996) to assess the effects of trophy hunting on two population-level parameters: stable antler size distribution (i.e. the expected distribution of antler length per age-group within the population, SAD hereafter) and reproductive value (i.e. the relative contribution of an individual with a specific antler size to the future population, RV hereafter). We investigate the relationship between antler size and key demographic processes relating to the male component of the population (i.e. we ignore females). Our logic for doing this is that selective hunting is expected to change the relative reproductive value between males with different

antler sizes, and it is the relative contribution of individuals with different character values to future populations that is of interest if one is to understand the likely consequences of selective harvesting. We then construct the first IPM for the species (exclusively for males), from which we extract estimates of SAD and RV. Finally, we perturb the resulting IPM to simulate the effects of different harvesting regimes at the population and age-group levels.

STUDY AREA

The data used in this study come from the unmanaged red deer population in the North Block of the Isle of Rum National Nature Reserve (578019 N, 068179 W; NM-402996), Scotland. The 10,600 ha island has a mild, wet and windy oceanic climate. Rainfall varies widely across the island, but April is generally the driest month whilst November and January are the wettest (see Clutton-Brock et al. 1982). Rum it is a mountainous island characterized by productive valleys, including extensive grassland cover closer to seashores, while fen vegetation prevails on higher elevations (Virtanen et al. 2002; Ball 1987).

In 1972, the routine 14% red deer cull of the North Block stopped and a long-term, individual-based investigation into behaviour, evolution, life history and population dynamics was initiated (Clutton-Brock 1981, Pemberton et al. 1996). Females give birth in May and June each year, and since culling stopped, approximately 90% of calves born in the North Block have been caught, individually marked and followed throughout their lives. Although all breeding attempts and deaths are recorded within the study area, animals that emigrate to other parts of the island cease to be monitored and their whereabouts are thereafter often unknown (Clutton-Brock et al. 1982).

Male red deer grow antlers annually from the age of 1 or 2 years old (Kruuk et al. 2002). Antlers are used in male-male encounters once the individual is sexually mature (at 3 to 4 years of age), even though they are unlikely to sire any offspring until they are 4 or more years of age (Nussey et al. 2009; Kruuk et al. 2014). Males cast their antlers annually

between March and May (casting season), following which they grow a new set of antlers until August. These lose their velvet (they are ‘cleaned’) around September prior to the start of the rutting season. To fit in with antler growth, the ‘deer year’ in our study runs from the 1st of August to the 31st of July of the next year. This ensured that only pairs of antlers used during the latest rutting season were assessed in relation to male calves recruited the following year.

METHODS

Antler measurements

Antlers were recovered in the field during the casting season of each study year and identified to individual-level by observation. Previous genetic analysis has suggested this method is 93% accurate (J.P. Petley and J.M. Pemberton, unpublished data). Antler length, weight and the number of tines, in addition to genetic samples and other measurements, were collected in the field (for more details see Kruuk et al. 2002 and Walling et al. 2010). Genetic samples were used to construct a multigenerational pedigree, in which paternity was estimated using genetic (genotypes at up to 15 microsatellite loci), phenotypic and behavioural data (see Kruuk et al. 2014). We focused on the length of antlers, which we use as an indicator of antler size. Importantly, antler length is one of the main characters targeted during trophy hunting activities.

Antler length was measured as the distance from the coronet to the furthest tip of the main beam, around the curves (Fig. 1). Where measures from both antlers (left and right) were available for the same individual for a given casting season, the average was used. For juveniles (i.e. individuals from 1 to 3 years old), antlers are often simple spikes. Spike length of living male calves was estimated by eye in the field. For any one male calf, multiple observers (2-4) estimated spike size using the ear length of the same individual as a reference. Observed spike length was taken as the consensus between observer measurements. As for

antlers, we used the average between left and right spikes when both were recorded.

Individual information was organised in a file with equivalent structure to that used in

Coulson (2012) (see Appendix A).

Construction of IPM and statistical analysis

Since only individuals that have reached reproductive maturity are able to defend

harems and reproduce, both antler size and reproductive status can be expected to vary

between male life stages. Consequently, we included age class as a factor in our analyses.

Considering that environmental variation imposes different selective forces on individual

survival and reproduction, we grouped males into four reproductive and four survival age

classes. Reproductive age classes consisted of juveniles (individuals between 1-3 years old),

young adults (individuals of 4 to 6 years old), adults (individuals of 7 to 11 years old) and

seniors (individuals of 12 years and older). Survival age classes consisted of calves

(individuals between 0-1 years old), juveniles (individuals between 2-3 years old), adults

(individuals between 4-8 years old) and seniors (individuals of 9 years and older). In both

cases, age classes were based on Kruuk et al. (2002), with the exception of the adult age

class, which in our case was extended to include individuals of four years old since these

were observed to reproduce in our study population. Both age classifications were used in our

model.

IPMs are composed of four fundamental functions describing the processes of

survival (S), recruitment (R), growth (G) and parent-offspring trait correlation (D)

(inheritance, hereafter), which together predict, in this case, the distribution of antler length

(l) per age-class (a) at time $t + 1$, as a function of antler length at time t (e.g. see Ozgul et al.

2010; Traill et al. 2014). Together, these predict the distribution of the number (n) of

individuals with antler length (l) per age-class (a) at time $t + 1$, as described by the

following equations:

$$n(1, t + 1, l') = \sum_a \int dl D(l' | l) R(a, l) n(a, t, l) \quad \text{eqn1}$$

$$n(a + 1, t + 1, l') = \int dl G(a, l' | l) S(a, l) n(a, t, l), a \geq 1 \quad \text{eqn2}$$

Equation 1 describes the distribution of offspring antler length at time $t + 1$, which is calculated from both, the number of offspring produced by a male with antler length l per age class (i.e. $R(a, l)$) and the correlation between paternal length at age a and offspring antler length at age 1 (i.e. $D(l' | l)$). Together these describe the probability that an individual with antler length l at time t of age a will produce a son with antler length l' at time $t + 1$. Additionally, $R(a, l)$ includes the product of fertility (R_F), which describes the probability that a male will reproduce or not, and the number of offspring produced from those individuals that do reproduce (R_N). In our model, only individuals over 4 years old (i.e. males producing offspring) were considered in the reproduction analysis.

Eqn 2 describes the probability that an individual of age a and antler length l will survive from time step t to time step $t + 1$ (i.e. $S(a, l)$). The growth function (i.e. $G(a, l' | l)$) describes the growth of antler from l at time t to l' at time $t + 1$ of individuals from an age class a . Both functions in eqn2 describe the distribution of antler lengths from individuals that survive from one time step to the next one. Below, we describe how each of the four fundamental functions was parameterized and statistically analysed.

1. Antler length - survival (S): We performed a mark-recapture (MR) analysis in order to test for the effect of age and antler length on male survival, while accounting for imperfect detection of individuals (Lebreton et al. 1992). We considered a Cormack–Jolly–Seber (CJS) model (Lebreton et al. 1992) with two states to describe the fate of an individual (1 = alive; 0 = dead), and two events to describe the observation process (0 = antler not found, 1 = antler detected). At each time step t , an individual can be alive with probability S_t , and its antler can be found with probability P_t .

We first performed goodness-of-fit tests starting from a general CJS model allowing survival and detection probabilities to vary with time (Lebreton et al. 1992) using program U-CARE (Choquet et al. 2009). We detected a lack of fit due to ‘transience’ (i.e. individuals in transit across the study area) and ‘trap-happiness’ (i.e. individuals caught once are usually more likely to be caught again) effects (Pradel et al. 1997) due to antlers being found, or not found, in the field. Once we had accounted for the presence of transient individuals, the over-dispersion coefficient due to the ‘trap-happiness’ effect was acceptable ($\hat{c} = 2.48 < 5$) (Burnham & Anderson 2002). To account for the ‘transient’ effect, we considered a two age-class structure for survival (Pradel et al. 1997), whereby individuals were defined as being either juveniles (i.e. calves and juveniles from the IPM age-classes) or adults (i.e. adults and seniors from the IPM age-classes). This choice is sensible since younger individuals tend to stay with their mothers (and therefore within the study area) in their first two years whilst older males disperse across the island. Thus, using a CJS model that included a time-varying individual covariate (following Choquet & Nogue 2011), we tested for additive effects and an interaction between age class and antler length on survival. Collinearity was not an issue here, even when the range of antler length varied within age classes as well as its relationship with survival, since age was used as a group as illustrated in Fig. 2. We also tested for an effect of age on detection probability. Models were fitted using program E-SURGE (Choquet & Nogue 2011). Standard maximum likelihood procedures were used to obtain parameter estimates (Lebreton et al. 1992). Model selection for the MR analysis and each fundamental function of the IPM were based on Akaike’s Information Criterion (AIC) (Akaike 1973). R v3.0.1 was used for all statistical analysis (R Core Team 2014).

We used estimates for the intercept and slope from the best model to parameterise the survival function of the IPM:

$$S(a, l) = \frac{1}{1 + e^{-(\alpha_{S,a} + \beta_{S,a} l)}} \quad \text{eqn3}$$

Here, an individual from age class a and antler length l at time t has a probability of survival of $S(a, l)$. $\alpha_{s,a}$ and $\beta_{s,a}$ denote the intercept and slope per age-class, respectively.

2. Antler length - recruitment (R): We used generalized linear models (GLMs) to estimate male fertility (i.e. the probability for an individual to reproduce or not in a given year, R_F hereafter) and the number of recruits produced per male (R_N) once he reproduces, each as a function of antler length and age class. R_F was estimated from a GLM with a binomial error and logit link function and had the same structure as $S(a, l)$ but with $\alpha_{F,a}$ and $\beta_{F,a}$ representing intercept and slope for fertility, respectively.

$$R_F(a, l) = \frac{1}{1 + e^{-(\alpha_{F,a} + \beta_{F,a} * l)}} \quad \text{eqn4}$$

R_N was modelled using a Poisson error structure and a log link function, because of the count nature of our data. The R_N function within the IPM takes the following form:

$$R_N(a, l) = e^{-(\alpha_{N,a} + \beta_{N,a} * l)} \quad \text{eqn5}$$

This function describes the number of offspring that individuals from age group a , and of antler length l , will recruit conditional on reproduction into the population at time t . In eqn5, $\alpha_{N,a}$ and $\beta_{N,a}$ are the intercept and slope per age-class, respectively.

If R_F is the number of individuals that reproduce per age group in the population and R_N the number of offspring that individuals that do reproduce contribute per age group, the final equation for the recruitment function corresponds to the product of both:

$$R(a, l) = R_{F,a} * R_{N,a} \quad \text{eqn6}$$

3. Antler length - growth (G): We combined two sources of information to determine the ontogenic development of antler length. First, we used a linear model to fit regression lines per age class within both age group classifications (i.e. survival and reproduction) between measures from males sampled at time step $t + 1$, in relation to the same individual at time t . The expected antler length at time $t + 1$ for a given antler length at time t had the

form $E(a, l) = \alpha_{g,a} + \beta_{g,a} * l$, where $\alpha_{g,a}$ and $\beta_{g,a}$ are the intercept and slope for individuals of age class a ; l is antler length at time t , and l' is antler length at time $t + 1$. We then squared the residuals from this first model and regressed them against the antler length in a second linear model. We obtained the following equation, $\sigma^2(a, l) = \alpha_{gv,a} + \beta_{gv,a} * l$, in which the variance intercept and slope per age group are represented by $\alpha_{gv,a}$ and $\beta_{gv,a}$ respectively. Finally, to estimate G in the IPM, we incorporated both functions in the following equation:

$$G(l' | l) = \frac{1}{\sqrt{2\pi\sigma^2(l,a)}} e^{-\frac{(l'-E(l,a))^2}{2\sigma^2(l,a)}} \quad \text{eqn7}$$

4. Antler length - inheritance (D): We compared the antler length of male offspring that survived from birth to their first census ($t + 1$), with that of their respective fathers at the time when the offspring was sired (t). One thousand nine hundred and ninety-two repeated antler measurements were collected from the field between 1970 and 2012, representing a total of 869 unique males. Of these, 388 had known male offspring at time step $t + 1$, with spike length measured on 29 of the latter. We used these available data to predict the spike length at age one of adults for which this measurement had not been taken, but which had been observed in later life stages ($N = 143$ out of 388). Offspring that died before age one and were not seen in later life stages could not be included in this analysis because it was not possible to estimate their spike length.

We used two linear models to estimate the inheritance function: one to regress antler length of offspring at time $t + 1$ against antler length of the males that sired them at time t (i.e. the mean); and another to determine the relationship between squared residuals and average antler length in the population (i.e. the variance). The final equation for D followed a Gaussian distribution in the IPM:

$$D(l' | l) = \frac{1}{\sqrt{2\pi\sigma^2(l)}} e^{-\frac{(l' - (\alpha_d + \beta_d * l))^2}{2\sigma^2(l)}} \quad \text{eqn8}$$

The model for D did not consider age classes because no statistical difference was found between age groups for this function. We therefore did not obtain intercepts and slopes per age class as in S , R and G . Here, only one intercept (α_d) and one slope (β_d) from the first linear model, and one intercept (α_{dv}) and one slope (β_{dv}) from the variance model (i.e. $\sigma^2(l) = \alpha_{dv} + \beta_{dv} * l$) were used to predict $D(l' | l, t)$ in the IPM.

Numerical implementation. — In order to construct the matrix approximation for the IPM, we first discretized a range of values for antler length between the minimum (0 cm) and maximum (93.8 cm). We considered values between 0 and 100 to create 200 bins separated by an interval of 0.5 cm. We used the *midpoint rule* (Ellner & Rees 2006) in numerical approximation of the integrals to implement the IPM. We constructed a projection kernel from the four fundamental functions. The latter was then discretized to obtain a matrix model from which parameters of interest were calculated by eigen-analysis, which in turn provided us with eigenvectors. These demographic parameters corresponded to: the stable antler size distribution (SAD) and the reproductive value (RV). Since we did not include females in our analysis, we standardized RV over all males (i.e. male population RVs summed to 1) for the entire study period.

Elasticity analysis

We performed an elasticity analysis to examine how SAD and RV responded to perturbation of parameters in the model. We independently increased each of the age class coefficients (i.e. intercepts and slopes) by 1%, meaning that positive and negative values were multiplied by 1.01 and 0.99, respectively. After each perturbation we re-ran the IPM, returning to the original coefficients before altering the next parameter. This process is a conventional way of assessing how demographic parameters of interest are influenced by small perturbations

(Easterling et al. 2000; Coulson et al. 2010). By perturbing each parameter we aimed to understand how that specific value affected transition rates in the sub-matrices within and between age groups, and how this change ultimately altered SAD and RV. If no changes in the demographic parameters of interest (i.e. SAD and RV) are observed between perturbed and unperturbed models, we would expect no association between antler size and the model predictions calculated from the IPM (Coulson 2012).

Harvesting analysis

To investigate the effects of harvesting on the male component of the red deer population, we simulated the removal of males under two scenarios: trophy hunting and uniform culling. For the purpose of this study, uniform culling was defined as the removal of a certain percentage of the population of males, regardless of antler length. In contrast, trophy hunting is a non-random process whereby humans select individuals to be removed based on one or several phenotypic traits (Festa-Bianchet 2003; Mysterud 2011). For the trophy hunting simulation, three proportions of males with antlers above a threshold length were removed from the population: 10%, 20% and 50%. We focused on these three harvesting values as these are known to represent an unusually low hunting off-take (10%), a threshold above which male red deer population size is known to decrease (20% - Clutton-Brock & Lonergan 1994), and an over-intensive harvest quota (50% - Clutton-Brock & Lonergan 1994; Clutton-Brock et al. 2002). Since trophy-hunting stalkers generally avoid shooting calves and juveniles, we fixed trophy harvest as a decrease in survival rates of individuals older than 4 years (i.e. adults and seniors).

We implemented the trophy hunting approach by targeting only individuals with antler lengths that were above the mean value for the antlered population (i.e. mean antler length – mAL hereafter – which was calculated from the unharvested male population). Accordingly, we multiplied the probabilities of survival for antler sizes above this threshold

by 0.9, 0.8 and 0.5. For each of these, we re-calculated SAD and RV from the IPM. We then asked the question: what harvest rates would we have to implement in the uniform culling approach to obtain identical values of mAL and RV than those obtained with trophy hunting? To do this, we obtained values of mAL and mean RV for a range of uniform culling rates (0 to 50%). We then regressed harvest rate against mAL, and mean RV and used the resulting equation to derive the required uniform harvest rate values for the whole population of males that have antlers. In addition, we also investigated potential reproductive compensatory responses of smaller antlered males once the biggest trophies were removed through trophy hunting (for more details see Supplemental Material, available online at www.onlinelibrary.wiley.com). To simulate this, we multiply the probabilities of recruitment of individuals with antler size above the threshold remaining in the population by 1.1, 1.2 and 1.5 respectively. For each of these, we re-calculated RV from the IPM. Finally, we standardized the resulting RV to better represent males' contribution per age group within the population.

RESULTS

Fundamental functions

Antler length had a positive influence on survival and recruitment rates (Fig. 2, rows a and c) with the exception of senior survival rates, which decreased with antler length. Survival in younger age groups (i.e. calves and juveniles) was positively correlated with antler length, although this relationship was found to be stronger in juveniles (Fig. 2, a.2). Adults with longer antlers were more likely to survive than those with shorter ones (Fig. 2, a.3). For seniors, increasing antler length was associated with a decrease in survival (Fig. 2, a.4).

The number of male offspring recruited per adult/senior male followed similar trends across age classes that were reproductively active (i.e. young adults, adults & seniors) (Fig. 2,

row b). Within reproductive age groups, the probability of recruiting offspring into the population increased with antler length ($X^2 = 400.78, p < 0.0001$).

Growth, measured as the association between antler length at years t and $t + 1$ showed positive trends ($F = 966.6, DF = 488, p < 0.001$) (Fig. 2, row c). However, as seen in figure 2, the regression lines cross the zero-growth line for all age classes, indicating that males with small antlers are expected to grow larger antlers next year, whereas those with large ones are expected to grow smaller ones. In other words, antler growth rate declines with antler size. In calves and juveniles, mean antler growth presented great variation around the regression line. For calves especially, mean antler size at $t + 1$ was as much as 35 times the size at t . Regression lines showed a much tighter fit in adults and seniors, reflecting a consistent growth of antlers for these age groups.

The inheritance function correlated father's antler length at siring to offspring antler length when recruiting to the population. As expected, the slope value for D was close to zero ($F = 1.602, DF = 167, P > 0.1$) (Figure 2, row d).

IPM demographic parameters

The corresponding age-structured stable antler size distribution (SAD) for the male population is shown in Fig. 3a. The SAD was characterised by a high proportion of males with small antlers (between 0 and 30 cm), representing the high percentage of calves and juveniles that grow small antlers during their first and second year (or do not grow them at all, i.e. antler length = 0). Representation in the population decreased with antler size (Fig. 3a), with very few individuals possessing antlers over 90 cm. The estimated mean antler length for adult and senescent males was 56.58 cm; which is similar to the average antler size calculated from the raw data (i.e. 56.08 cm).

The age-specific relative reproductive value (RV) for the male population is shown in Fig. 3b. The relative RV estimated by the IPM increased in relation to antler size (Fig. 3b).

However, the reproductive potential for age groups in which antler length increases rapidly (i.e. age classes of 1-3 years old) showed higher slopes than older age groups at equivalent antler sizes. Thus, the relative RV decreased proportionally in older individuals (i.e. ages classes over 8 years old) (Fig. 3b).

Elasticity analysis

Population mean antler length (mAL) and mean reproductive value (mRV) were sensitive to most function parameters (Fig. 4). The upward change in the intercepts and slopes of both the survival and growth functions had stronger effects on mAL and mRV than changes in any other function. Both were extremely elastic to changes in juvenile survival parameters (Fig. 4a.1 & b.1), this is not strange given that the effect of antler length on juvenile survival was significant. Perturbations to the growth function showed consistent positive effects on mAL. Antler length was primarily determined by changes in the adult group (Fig. 4a.2). Mean RV was particularly elastic to perturbed parameters associated with calf and adult antler growth (Fig. 4b.2), as well as to an upward change in adult parameters for the recruitment function (Fig. 4b.3).

Harvesting analysis

For simulated trophy hunts of 10, 20 and 50% of males with antler length greater than the population mean, the values for mAL were 55.90, 55.19 and 53.17 cm, respectively (Table 1), and corresponded to uniform culling rates of 11.9, 21.5 and 49.5%, respectively. The same trophy hunting resulted in population mRV values of 4.47, 4.20 and 3.42, respectively. These were equivalent to uniform culling rates of 35.3, 53.8 and 72.7% (table 1). As expected, the simulation of trophy hunting quotas of 10, 20 and 50% in our modified IPM skewed the SAD towards individuals with smaller antlers (Fig. 5a). In contrast, changes in mAL appeared to be very small.

Under the same harvesting simulation, the relative RV of individuals with antler length above the population mean experienced a rapid decrease (Fig. 5b). The removal of 10, 20 and 50% of males in the population also showed proportionally higher relative RV for individuals with shorter antlers (Fig. 5b). Overall, after the harvesting analysis, the mean rRV decreased with higher quotas of trophy hunting for adults and seniors (Fig. 6). Non-significant differences were found between the latter analysis and cases including reproductive compensatory responses from smaller antlered (Fig. S1).

DISCUSSION

The demographic consequences of selectively harvesting wild ungulates remain uncertain in spite of trophy hunting being a popular recreational activity worldwide (Milner et al. 2007; Palazy et al. 2011). The literature suggests that harvesting of males in mammals does not affect population dynamics significantly (Myserud et al. 2002). In other words, the population dynamics of males is determined to a large extent by the number of females. However, the phenotypic attributes of males in future populations are determined by the reproductive value of males, and the fidelity with which antlers are passed from parents to offspring. In addition, males are typically culled by fee-paying hunters and generate more income than females (Clutton-Brock et al. 2002). Taken together, these insights have led to the suggestion that harvesting of adult male ungulates for antler trophies may represent a sustainable conservation tool. The approach we present here, despite some limitations, has shown how integral projection models can be used to gain an understanding of the consequences of hunting on mRV, a measure of relative fitness, and the distribution of antler sizes within the population.

Under unmanaged conditions the fundamental functions of our IPM revealed – for some age classes – a noteworthy relationship between antler length and key demographic processes. Adults with larger antlers were more likely to survive and recruit individuals into

the population, a finding that is consistent with the notion that antler size reflects the health of an individual (Hamilton & Zuk 1982; Andersson 1994; Malo et al 2005b), as well as confers higher reproductive success (Clutton-Brock 1988; Andersson 1994; Kruuk et al. 2002). A stag's ability to defend harems is closely related to its ability to win fights (Clutton-Brock et al. 1979; Clutton-Brock et al. 1981; Clutton-Brock 1988), and it can be expected that individuals with smaller antlers have a higher risk of being evicted from potential territories – and thus a reduced probability of holding harems (Carranza et al. 1990) – or being injured during the rut. While we exclusively consider demographic processes as drivers of antler size, Kruuk et al. (2002) found the same relationship between antler size and breeding success for males of the same population after accounting for environmental effects. Given these pronounced associations, trophy hunting has the opportunity to impose considerable impact on the male component of the population. However, our study revealed that this was not always the case.

Inheritance, or the correlation between the parental trait at age a and the offspring trait at age 1, was low. This function should not be confused with heritability (e.g. see Coulson 2012). Previous studies have shown that antler size has a low heritability within this red deer population (Kruuk et al. 2002 & 2014). It is important to stress that the inheritance function in our study was particularly susceptible to measurement error resulting from the estimation of spike length for some individuals. Additional biases may also have arisen from male calves failing to survive to later ages. However, we do not believe our results to be strongly impacted by these potential biases as the responses of mean antler size and reproductive value to changes in the inheritance function parameters were relatively small.

Our results show that mean antler size is highly elastic to parameters in the growth function. This is unsurprising, as in order to evolve a larger or smaller trait, it is necessary to alter how long an individual develops the trait for, or the speed at which the trait develops. In

contrast, the reproductive value of individuals was most elastic to the survival function. In a long-lived species like deer, population growth rate, a measure for population-level fitness is usually most sensitive to survival rather than fertility (Coulson et al. 2004). In agreement with this we report that relative reproductive value and mean antler sizes are sensitive to selective harvesting only when culling rates are as high as 50%. These results suggest that lower levels of trophy hunting are unlikely to have a large effect on key aspects (i.e. survival and reproduction) of hunted populations and are in agreement with conclusions from previous studies (Mysterud 2011; Traill et al. 2014).

Our results were obtained from a simple model. Firstly, we did not include the female component of our study population. This precluded us from studying aspects of population dynamics in a system that is largely female dominant. Females do not develop antlers and no maternal effects have been found to significantly influence antler size (Kruuk et al. 2002, Kruuk et al. 2014). Therefore, we do not explicitly model this aspect of our study system. Because of the above, we do not expect our focus on males to be entirely inappropriate.

Our model did not include the effects of density dependence or environmental stochasticity, both of which are known to play important roles in shaping population dynamics (Coulson et al. 2004) and antler development. The nutritional consequences of increased population density are influential in determining antler size in red deer (Clutton-Brock & Albon, 1989; Kruuk et al. 2002; Schmidt et al. 2007). In deer species, habitat quality influences not only the absolute but also the relative size of antlers (Ramanzin & Sturaro 2014), and males are more susceptible to bad weather conditions than females (Pelletier et al. 2012). Selective culling experiments have shown that reductions in hind density often lead to increases in stag numbers (Clutton-Brock et al. 2002). However, for sexually dimorphic species, it remains unclear whether males are sensitive to either female or male densities, or a combination of both (Bonenfant et al. 2009). Therefore – and because the focus of our study

was to investigate purely demographic effects of selective hunting on mAL and RV – including density dependence and environmental stochasticity would have limited our ability to attribute our results to hunting exclusively. Nevertheless, we are aware these are important variables in determining demographic parameters in wild populations and suggest that future models should include them in order to obtain results more illustrative of the effects of trophy hunting on wild populations of red deer.

MANAGEMENT IMPLICATIONS

Integral projection models offer a powerful tool for understanding the phenotypic and life history consequences of harvesting (Bunnefeld & Keane, 2014; Traill et al. 2014). Our study offers valuable insights into how trophy hunting may influence reproductive value and mean antler size in red deer at unusually high hunting quotas (more than 50%). Our findings lead us to the tentative conclusion that a trophy hunting rate between 10% and 20% is unlikely to have a substantial impact on mean antler size.

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Figure Captions

Figure 1. Antler length measurement. The white dotted line shows the distance between a) the antler coronet and b) the highest point of the mean beam around the curves.

Figure 2. Relationship between antler length (cm) and four fundamental demographic processes: a) survival, b) recruitment, c) antler growth, and d) inheritance (as a function of offspring antler length at time step $t + 1$). Survival and antler growth age classes consist of calves (0-1 years), juveniles (2-3 years), adults (4-8 years) and seniors (older than 9 years). Reproductive and inheritance age groups consist of juveniles (1-3 years), young adults (4-6 years), adults (7-11 years) and seniors (older than 12 years). In all panels shaded areas indicate the 95% confidence intervals.

Figure 3. a) Stable antler size distribution (SAD) of antler length per age class. Each line represents the antler size distribution associated with ages 1 to 13 (see numbered labels). The inset plot shows the additive SAD for the whole population. b) Relative reproductive value (rRV) as a function of antler length per age class. Each line represents the antler size distribution attributed to ages 1 to 13 (see numbered labels). Solid lines denote rRV distributions within age group antler length ranges, and dashed lines represent distributions predicted from the IPM for antler lengths out of age group ranges. The inset plot shows rRV for the whole population.

Figure 4. Sensitivity of population mean antler length (mAL) and mean reproductive value (mRV) to perturbation of IPM function parameters. Black and grey bars represent the change in mAL/mRV following perturbation to intercepts and slopes, respectively. Age classes for survival (a.1 & b.1) and growth (a.2 & b.2) functions are represented by: calves (0-1 year),

juveniles (2-3 years), adults (4-8 years), and seniors (older than 9 years). Age classes for the recruitment (a.3 & b.3) and inheritance (a.4 & b.4) functions are defined as: juveniles (1-3 years), young adults (4-6 years), adults (7-11 years), and seniors (older than 12 years).

Figure 5. Harvesting effects on a) the stable size distribution (SAD) and, b) the relative reproductive value (rRV) of male red deer in the study population. Grey lines represent a non-harvested population. Dotted, dashed and full black lines represent trophy hunting regimes of 10%, 20% and 50%, respectively.

Fig. 6. Change in relative reproductive value (rRV) per antler length and age class following different trophy hunting rates. Numbered lines represent antler size distributions associated with ages 1 to 13. a), b) and c) correspond to simulations of 10%, 20% and 50% of harvesting, respectively.

Table 1. Effect of equivalent rates (%) of uniform and trophy hunting on mean antler length (mAL) and mean reproductive value (mRV).

Trophy hunt	Resulting mAL (cm)	Equivalent uniform cull - mAL	Resulting mRV	Equivalent uniform cull - mRV
10%	55.90	11.9	4.47	35.3
20%	55.19	21.5	4.20	53.8
50%	53.17	49.5	3.42	72.7

APPENDIX A: DATA FORMATTING

The data used in this project was individual-based information on males from the red deer population of the Isle of Rum, Scotland. Each row in the dataset corresponded to information of an individually identified male in a particular year of study between 1972 and 2012 (see Table A1 as an example).

Table A1. Example of data structure for two individuals of male dataset from the Isle of Rum.

Code	Cast year	Age	Survival	Reproduce	Num.males	Antler length (cm)
EID01	2000	9	1	1	5	80.4
HRM90	2009	9	1	0	0	70.9

The information per individual was organised similarly to Coulson (2012), with columns corresponding to:

- *code*: unique combination of names and numbers to individually identify males from the population.
- *cast year*: deer year running from the 1st of August to the 31st of July that indicates time t at which an individual cast its antlers.
- *age*: an integer representing the year of the male at time t . For instance a calf born in May 2000 (i.e. time t) would be one year old at anytime after August 2000 (i.e. time $t + 1$). Thus, when the same male cast his antlers in April 2004 (i.e. time $t + 4$), he was considered to be 4 years old.
- *survival*: survival of an individual determined by a “1” when a particular male was seen alive, and a “0” when the male was seen dead. This data was gathered between the 1st of August of year t and the 31st of July at year $t + 1$.

- *reproduce*: individual denoted with a “1” when produced a live male offspring and with a “0” when no male offspring were identified for the male at year t .
- *num.males*: number of male offspring recruited by a single individual at year t that survived to recruit to the population in August of year $t + 1$.
- *antler length*: the length of antlers (cm) collected during the casting season (March to May) at year t .

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